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May 28, 1857.

The LORD WROTTESLEY, President, in the Chair.

The CROONIAN LECTURE was delivered by JAMES PAGET, Esq., F.R.S., "On the Cause of the Rhythmic Motion of the Heart," as follows:—

I have selected for the subject of my lecture, the cause of the rhythmic motion of the heart; guided to this choice, partly by the belief that the Croonian lecture must have some relation to muscular motion, and partly by the interest which I have acquired in the subject in the course of observations extended, though with many and long interruptions, over some ten or twelve years.

It is not necessary that I should enter on any consideration of the various opinions that have been entertained on the cause of the heart's peculiar motion. Let me first show what it is, and how it differs from the other motions in the same body, which are visible to the naked eye.

In a beheaded tortoise, or any other of the Amphibia, the muscles of the trunk and limbs are usually in perfect rest, unless disturbed: those in the head may act so as to produce a kind of gasping and swallowing movements, at distant and nearly regular intervals (an imperfect kind of rhythmic motion): the digestive and other mucous canals are at rest, or move with slow worm-like actions; but the heart maintains, with perfect regularity, the rhythmically alternate contractions and dilatations of its auricles and ventricle; its several movements being ordered, not only in the manner of their succession, but in rhythm, *i. e.* in the proportions of time which they severally occupy.

Why is this difference? To what may we refer as the cause of this apparently peculiar mode of muscular movement? In answer, let me show (for it is a condition of the Croonian foundation that experiments should be shown) that the cause of the rhythmic action is in the heart itself; not in any of the great nervous centres through which other muscular movements are excited, including those in the

separated head, which will cease at once on destruction of the medulla oblongata and brain.

The evidence of this is in the continued action of the heart after it is cut out of the body. It may remain at rest for a few minutes after the excision; but then, as if recovering from shock or fatigue, it again begins to act, and thus will continue for many hours acting as regularly as it did when its connexions were unbroken.

The time during which the action of the cut-out heart will be maintained is different in the several classes of the Vertebrata; but some such continuance may be observed in all, and in all the experiment is enough to prove that the rhythmic action does not depend either upon distant nervous organs, or upon the blood which naturally flows through the cavities of the heart; for as soon as the heart is cut out, its cavities are emptied and no blood flows through them.

Thus, then, for a first conclusion, we may be sure that the cause of the rhythmic action of the heart is something in the heart itself; and this, notwithstanding the variations of the rhythm, which may be produced by morbid or artificial states of organs far distant from the heart.

But the cause, whatever it be, is not equally in all parts of the heart; for when its parts are in certain manners separated, some continue to act rhythmically, and others cease to do so. If, for example, the cut-out heart be divided into two pieces, one comprising the auricles and the base of the ventricle, the other comprising the rest of the ventricle, the former will continue to act rhythmically, the latter will cease to do so, and no rhythmic action can be, by any means, excited in it. The piece of ventricle does not lose its power of motion, for if it be in any way stimulated, it contracts even vigorously; but it never contracts without such an external stimulus, and, when stimulated, it never contracts more than once for each stimulus. Without losing motility, it has lost all rhythmic power, and all appearance of spontaneous action. We can, indeed, make it imitate a rhythm by stimulating it at regular intervals, such as every two or three seconds; but in any experiment of this kind, it will presently appear how much sooner the motor force is exhausted by the artificially excited actions, than by the apparently equal actions of the natural rhythm.

Other sections of the heart, and experiments of other kinds, would show that the cause of the rhythmic action of the ventricle, and probably also of the auricles so long as they are associated with it, and not with the venous trunks, is something in and near the boundary-ring between the auricles and ventricle; for what remains connected with this ring, or even with a part of it in a longitudinally bisected heart, retains its rhythm, and what is disconnected from it loses rhythm.

An experiment related by Heidenhain*, seems to show more precisely where the source of the rhythmic action of the ventricle is seated. If the ventricle of a frog's heart be separated, and every part of the septum of the auricles be removed from its base, so that its cavity may be perfectly single; and if, then, it be set upright on a board with some blood in its cavity and around it, it will be found that as pieces are cut away from its upper border, so its pulsations become less and less frequent, till at length, when a zone of a certain depth has been removed, they cease altogether. The depth of the zone to be cut away may be nearly one-third of the length of the ventricle; and somewhere in this zone we must assume lies that on which the rhythmic action of the ventricle, when alone or with part of the auricles, depends.

But wherever may be precisely the sources or centres of the rhythmic action of the heart, or any of its parts (and most of these details, I think, have yet to be determined, even for the hearts of Amphibia, and much more for those of other orders), these experiments seem enough to prove that the rhythm does not depend on the properties of the muscular tissue alone or independently. If it were so, it would be highly improbable that certain portions of the heart being separated should lose rhythmic action, and others just like them, so far as their muscularity is concerned, should retain it.

This conclusion is confirmed by many experiments invented by Professor Stannius†, and often repeated by myself and others, with results varying little from those which he obtained.

Perhaps the most remarkable of them is, that if a ligature be tied tightly round the place of conflux of the great veins entering the

* Quoted in Canstatt's 'Jahresbericht' for 1855, p. 130, from his "Disquis. de nervis organisque centralibus ocrdis." Berlin, 8vo.

† Müller's 'Archiv,' 1852, p. 95.

auricles of a frog's or tortoise's heart, the rhythmic action immediately, or after a few beats, ceases, and is suspended for three or many more minutes, and then returns in the ventricle alone (I believe) at a much slower rate than it had before.

This result is not due to the stoppage of the flow of blood into the heart, for if the veins be tied separately at a distance from the auricles, the rhythm continues. Neither is it due to the loss or great diminution of mere motility; for if the heart thus brought to rest be stimulated, it acts once, or rarely more than once, its action travelling from the part stimulated over all its substance. The result seems due to an injury done to something beneath or behind the ligature, from or through which some influence would naturally be conducted from the conflux of the veins to the auricles, and thence to the ventricle; for in the other direction, *i. e.* in the trunks of the veins behind the ligature, even to a great distance from the auricle, rhythmic motion still continues, and is scarcely, if at all, changed. And by variously placing the ligature, it would be found that, where-ever tied between the venous sinus and the auriculo-ventricular ring, all the parts behind it would retain, and all those before it would lose (at least, for a time), their rhythm.

This indication of the experiment (that the loss of rhythm, namely, depends on injury of something beneath or behind the ligature) is confirmed by another, whose whole import, however, I am quite unable to explain.

If, when a heart is thus brought to rest by a ligature tied round the conflux of the veins, another ligature be tied round the boundary ring of the auricles and ventricle, and including the bulbus arteriosus of the frog, or the two aortæ of the tortoise, the rhythmic action remains suspended in the auricles, but at once begins again in the ventricle, or, if it have not wholly ceased there, is much accelerated. We thus obtain a condition of the heart in which the great veins and the ventricle act rhythmically, though not with the same rhythm, but the auricles between them are at rest.

Now, in all these facts there appears sufficient evidence that the source of the rhythmic action of the heart is not in the muscular structure alone, or in its relation with the blood in the cavities, or in the vessels of the heart; for these things are not in any of the experiments more disturbed in one part of the heart than in another.

The nutritive relations of the muscular tissue and the blood are sufficient for the maintenance of mere motility, but they are not sufficient for the maintenance of rhythmic motion; they can maintain the power of acting upon external stimulus, but cannot give spontaneity of action, or regulate the time or manner of acting.

It is interesting to observe in these experiments three different modes of action of the heart: (1) the truly rhythmic, in which the contractions of its several parts, or of some of them when separated, ensue spontaneously (*i. e.* without evident stimulus or change of external conditions), and observe a definite order and proportion of time; (2) such as may be excited by stimulus, which, beginning at the cavity stimulated (whichever it may be), are effected simultaneously, or with a scarcely appreciable difference of time, by all parts of the walls of that cavity; then follow, with a certain interval, in the other cavities; and then are not repeated in the same order, but give place to the true rhythmic action, which they may for once have prevented or inverted; (3) those which ensue on stimulus, when the heart or any of its parts is utterly exhausted, and which commence at the point stimulated, and thence slowly travel once to all other points connected with it by continuity of muscle.

Now, of these three modes of action, the last may be ascribed to mere motility, such as the intestines and the stomach have, and such as is maintained by the nutritive relations of the muscular substance and the blood in its vessels. The second may be due to the same, acting with more energy; or it may be ascribed, as by Bidder* and Rosenberger†, to the action of reflecting nervous centres in the ganglia of the heart. But what of the third, the rhythmic, which every experiment shows to be essentially different from both of these?

It is explicable, and all the experiments are consistent, on the belief (which many before me have entertained) that it depends on certain nervous centres in the nerve-ganglia of the heart; which centres, by spontaneous discharges of nerve-force, cause the muscular structures to contract. These centres (rhythmic centres as they have been called) being injured or hindered in their operation, the rhythm ceases, though the motor power is not lost; or these centres, being cut away with certain portions of the heart, the other portions cease to

* Müller's 'Archiv,' 1852, p. 163.

† De centris motuum cordis. Dorpat, 8vo, 1850.

have rhythmic motion, though still capable of repeated single actions when artificially stimulated.

Such nervous centres may exist among the numerous ganglia in the heart, and the indications of their position in the frog's heart given by the experiments, agree very well with the dissections by Bidder and Rosenberger. There is, indeed, nothing in the structure or aspect of the ganglia presumed to be rhythmic, which can make us sure that they can act as nervous centres of peculiar force, much less (if it were possible) that they must act rhythmically. But the assumption of such rhythmic nervous centres is justified, not only by its sufficiency as an hypothesis, and by its accordance with the existence of ganglia in the appropriate places in hearts, but by the analogy of the only other example of naturally rhythmic muscular movements in our own or any other mammalian economy,—I mean the respiratory movements. These are certainly determined in their rhythm by the medulla oblongata. It is true, they are greatly influenced as to their rate and force, though not as to their very existence, by external conditions, and are amenable in a measure to the power of the will; and the rate and force of their rhythm are much more dependent, than are those of the heart's, on the conditions of distant parts. Nevertheless, essentially and habitually, the medulla oblongata is not only the nervous centre, but the rhythmic nervous centre, of the respiratory movements. When a certain portion of it is destroyed, the proper respiratory rhythm ceases, and nothing can renew it, whatever stimulus or variety of external conditions be present. Any of the respiratory muscles may be again stimulated to contraction; some of them will again, and for a few times, contract repeatedly and at regular intervals, imitating the old rhythm*; but there is no longer any combination or timely succession of the movements of the many respiratory muscles, as for their proper purpose.

* Such surviving rhythmic movements of the respiratory muscles may, perhaps, be ascribed to the continuance of the rhythmic nutrition, of which mention is made in a later part of the lecture, and which, though not the primary cause of their rhythmic action, must coexist with it; but other than the respiratory muscles may thus for a time act rhythmically when dying, or after their nerves are divided. See especially the observations of M. Brown Séquard in his 'Experimental Researches.' The facts may be very difficult to explain, but are not inconsistent with what I offer as the explanation of the rhythmic action of the heart.

In like manner, it may be that the rhythmic movements of the lymphatic hearts in Amphibia depend on a part of the spinal cord as their nervous centre; but this is doubtful*; doubtful I mean, not whether there be a nervous centre for the rhythmic movements, but where it is seated. The case of the respiratory movements, however, is clear, and should be reckoned as of great weight in the argument for the nervous origin of the heart's action.

The experiments on the heart's action which I have shown, have been selected as the simplest and most significant. I pass by many more, and say concerning them only this,—that I believe there are none whose results are inconsistent with the belief that I have expressed as to the cause of the rhythmic action of the heart. There are some, of which the results are difficult to explain; but the difficulties relate to questions of nerve-physiology†, and do not affect the simple conclusion that the rhythmic action of the heart in the Vertebrata depends on the operation of nervous centres in the ganglia on or near the substance of the heart: I say, in the Vertebrata; for as yet we know (I believe) nothing of the origin of the corresponding movements in the Invertebrata, though we may well believe that in them, and especially in the lower among them, the rhythmic movements of any pulsating vessel, analogous to a heart, are independent of any nervous system. Such a difference in the two great groups would correspond with similar differences in nearly all other parts of their several economies. The more highly developed the nervous system is, the more are its operations influential in those of every other part and system; and, for the heart, we may suppose that the making-over of its rules of action to a proper nervous system is on purpose that it may the more quickly correspond and sympathize

* See the Experiments of Schiff, Mayer and Budge, in Canstatt for 1850, p. 126; and those of Heidenhain in the same, for 1855, p. 130.

† I refer, especially, to those on the pneumogastric nerves, of which the continued galvanic stimulus stops the heart's action. The phenomena observed in this and similar experiments appear to me very similar to those of *shocks*. As a violent shock of any kind may exhaust the power, or suspend the action, of the brain or spinal cord, so may a shock by violence or galvanic force similarly affect the power of the rhythmic nervous centres for the heart. And the general explanation of all may be, that the nutrition of a nervous centre, and thereby the maintenance of its power, requires rest, and that this rest cannot exist while nerves in relation with it are under irritation.

with other organs, with which, but for their connexion through the nervous system, it could only sympathize more slowly through the medium of the blood.

But, now, it will not have escaped you to question,—why are these nervous centres rhythmic in their action? granting all that has been said, why is it that these nervous centres accumulate and discharge nerve-force, as it would seem, not only spontaneously, but at time-regulated intervals? To put on them, rather than on the heart's muscles, the work of rhythm, is only to put the real difficulty of the matter a step further back.

This is very true; and I will add, that they who hold that the rhythmic, like the ordinary, action of muscles, cannot ensue without stimulus, are in the like predicament, at a step still further back; for how, it may be asked, is the stimulus (of the heart suppose) applied or generated at regular intervals? And the difficulty is not in the case of the heart alone, but in that of all the rhythmic muscular movements. For why, it may be asked, does the medulla oblongata rhythmically excite the respiratory muscles into action? and if it be answered that it is itself stimulated by venous blood, or by impressions on the pneumogastric and other centripetal nerves, then how does the venous blood, or any other substance, thus rhythmically and not constantly stimulate? Constant stimulus, or constant production of an excess of nervous or muscular force, might produce constant muscular action, whether continuous or disorderly, but could not alone maintain a regularly interrupted action, in which the lengths of time of action and of inaction are in definite proportion.

This shifting of the question as to the cause of rhythmic motion suggests that we should enter on a larger inquiry, and take notice of whatever organic processes are performed with rhythm; and this seems the more necessary, while we consider that rhythmic action is not tied to any particular structure, whether muscular or nervous, nor employed in only one or two purposes, as blood-movement or breathing; nor even limited to the animal kingdom: so that, really, the peculiarity we have to study is not one of force, or not one of force alone, but one of *time* as an element in the organic processes. No explanation of the rhythmic action of the heart, therefore, would be sufficient, which did not involve or appear consistent with some general law to which we may refer all other rhythmic organic pro-

cesses, that is, all such as are accomplished with time-regulated alternations, whether of motion or any other change.

Probably, the simplest example of rhythmic motions yet known is that detected by the acute researches of Professor Busk* in the *Volvox globator*. At a certain period of the development of this simplest vegetable organism, there appear, in each zoospore, or in the bands of protoplasm with which the zoospores are connected, vacuoles, spaces, or cavities, of about $\frac{1}{9000}$th of an inch in diameter, which contract with regular rhythm at intervals of from 38 to 41 seconds, quickly contracting and then more slowly dilating again.

The observations of Cohn†, published about a year later than those of Mr. Busk, but independent of them, discovered similar phenomena in *Gonium pectorale* and in *Chlamydomonas*, the vacuoles, like water-vesicles, contracting regularly at intervals of 40 to 45 seconds. The contractions and the dilatations occupy equal periods, as do those of our own heart-ventricles; and in *Gonium* he has found this singular fact, that when, as commonly happens, two vacuoles exist in one cell, their rhythms are alike and exactly alternate, each contracting once in about 40 seconds, and the contraction of each occurring at exactly mid-distance between two successive contractions of the other.

Here, then, we have examples of perfect, and even of compound, rhythmic contractions in vegetable organisms, in which we can have no suspicion of muscular structure, or nervous, or of stimulus (in any reasonable sense of the term), or, in short, of any one of those things which we are prone to regard as the mainsprings of rhythmic action in the heart.

The case of ciliary movements is as simple; the cilia having a perfect rhythm, so that their alternate and opposite movements are of definitely proportioned length; and that, where many move on the same surface, they all keep time precisely, by moving, not all simultaneously, but in time-regulated succession. Here, too, we have no trace of muscular or nervous structure, or of stimulus; yet there is a perfect rhythm in which even myriads of cilia keep time,

* Transactions of the Microscopical Society of London, May 21, 1852.

† Untersuchungen über die Entwickelungsgeschichte der mikroskopischen Algen und Pilze. Breslau, 4to, 1854.

although there is no evident connecting medium between them, nor, generally, any continuity of structure.

I cite these two instances—the ciliary motion and the contraction of the vacuoles or vesicles in the minute Algæ,—as the simplest examples of rhythmic movements—simplest in regard of method, of structure, of apparent uniformity of circumstances, and of spontaneity. And if I were to enumerate all the instances of rhythmic motion that I can find, other than those of hearts, their variety would suffice to show, that for the explanation of rhythm, we must find something much wider than any peculiarity in the structure or nerve-supply of hearts. The time-regulated movements of Oscillatoriæ and their congeners; those of the lateral leaflets in *Desmodium gyrans,* and of the labellum in *Megaclinium falcatum**; the movements of spermatozoa and of their analogues in the vegetable kingdom; the constant rhythm of the nutritive yelk in the ovum of the Pike†; the movements of the pulmograde Acalephæ; the rhythmic actions of the larger veins in the Bat's wing:—all these make a heterogeneous list if we look to structure or to office; their only apparent mark of resemblance is that they are all rhythmical in action, *i. e.* they all observe a rule of time in the manner of their action, a rule in which there is a regulation not only of the times at which successive and alternate actions follow one another, but of those during which each action is continuous.

But there is another thing common to all rhythmically acting organs: they are all the seats of nutritive processes; and I believe that their movements are rhythmical, because their nutrition is so; and rhythmic nutrition is, I believe, only a peculiar instance, or method of manifestation, of a general law of Time as concerned in all organic processes. In other words, I believe that rhythmic motion is an issue of rhythmic nutrition, *i. e.* of a method of nutrition, in which the acting parts are at certain periods raised, with time-regulated progress, to a state of instability of composition, from which they then decline, and in their decline may change their shape, and move with a definite velocity, or (as nervous centres) may discharge nerve-force.

Regarded as phenomena of nutrition, the chief things in which

* Lindley; and Morren in the 'Annales des Sciences Naturelles.'

† Reichert in Müller's 'Archiv,' 1857, p. 46.

rhythmic changes, whether attended with motion or not, may seem strange, are (1) that they are not continuous, but interrupted, and, as it were, alternating between action and inaction, or between progress and regress; and (2) that they are very minutely observant of time. But, in both these regards, they are examples of very general laws of organic processes; alternations of action and of rest, or of opposite actions, being common phenomena of organic life, and all organic processes being regulated with exact observance of time.

In all organic processes, laws of time are observed as exactly as are those concerning weight, and size, and composition.

In the largest view, in that cycle of mutations, according to a parental type, in which the life of every individual (at least among the higher organisms) consists, the successive changes are accomplished with the same exact regard to time as to every other particular. The offspring at each period of its course attains the same condition as the parent at the corresponding period had attained; the rules of weight, of shape, of composition, and of time, are all alike observed in the reproduction of the parent in the offspring.

And, within this view, we may observe how all the parts, or even all the elemental structures, of any organism, keep time in its development. Prematurity is, probably, even more rare than is preponderance, among them.

And so to natural death; for rare as it may be, there is a death even among men, in which, with uniform and synchronous decay, all parts arrive at the same time at the stage of incapacity for work.

It is the same everywhere. How evident is the observance of a law of time in the organic phenomena of the seasons! or, with more minute regulation, in those of sleep and waking, not only among animals, but, much more exactly, in the leaves and flowers of plants; or in their unfoldings; or in the movements of stamina, the dehiscence of fruits and the like, whether in succession or coincidently! In all of these, occurring as they do precisely when they are necessary for the welfare of the individual or the race, we may observe a time-regulation of the organic processes, which, for its precision, passes calculation. For though many of these processes may be very dependent, as to the variations of their rate, upon external conditions, and especially upon variations of light and heat, yet their mean or proper rate is not explained by these conditions, nor is wholly

due to them; a distinct law of periodicity, various according to the species, is observed in all; and even what the external conditions do effect, they effect by their influence on processes of cell-life, which they can alter in respect of time in only the same measure, and with the same limitations, as they can alter them in respect of quantity, or any other character.

Instances of the time-regulation of processes in the animal economy are as evident: witness the returns of thirst and hunger, the regulated times for digestion, the rates of excretions, the daily risings and fallings of temperature, the times for the development of ova, for the growth and development of the uterus, and of all the parts appertaining to gestation and to lactation.

Equally is time observed in processes of disease. It is most evident, in one sense, in all intermittent and other periodic affections; but, in another way, as evident in eruptive fevers. In small-pox, for example, not only is the time set in which the complicated process of eruption will be achieved, but, though every pustule is, in its appearance, independent of the rest, yet all are together in regard of time, because there is the same time-regulation for all. And so, when we watch the progress and the natural remedy of some spreading disease, such as erysipelas or gangrene, the observance of time is, in the whole process, as exact as that of quantity, or any other characteristic of the disease.

I dwell the more on these facts, because, familiar as they are to all, their importance as indicating a general law of organic life seems to be overlooked, and especially their bearing on the explanation of the rhythmic action of the heart has not been duly considered. For not only are many of the processes to which I have referred instances of regular and time-ordered alternations of action, and therefore, in the strict sense, rhythmical; but they are all instances of that exact observance of minute periods of time, which, on a superficial view, appears as the most singular and inexplicable character of the rhythm of a heart. For, in all these cases, the final correctness of the result of the organic process, the punctuality of its event, is proof that it was exactly timed in every stage; that it was, throughout, regulated to the second; just as the action of the heart is, or as the accuracy of a chronometer, at a year's end, is proof, or very nearly proof, that it kept right time in every hour and every second

of the year. In the maturation or the development of an ovum, for example, or in the ripening of seeds, a law of time, various in different species, is observed by all, and their punctuality in arriving at the climax of maturity, after many hours or days or months of progressive change, is evidence that they were chronometric in all their course thitherward. And where many such processes are concurrent, though severally independent, as in the contemporary maturation of all the ovules of an ovary, we may say that their concurrence is like that of many exact chronometers; and their final punctuality, like that of the chronometers, would prove that, in each unit of time, each did a certain and proportionate amount of work.

In all organic processes, then, there is as minute a regulation of time as there is of quantity, or shape, or quality of matter. Time-work is not a singular characteristic of quickly rhythmic organs; it is a rule of life; and its rate in each organism is neither determined, nor beyond certain limits alterable, by external conditions, or by any appreciable qualities of weight or composition (as are the time-relations of inorganic masses); but is determined by properties inherited, and inherent in the very nature of the organism, and is least alterable by external conditions in the highest organisms.

But though the general law of chronometric nutrition (if I may so call it) may be evident, yet it may be objected by some, that it is proved only for such nutritive processes as are long-continuous and cumulative; and that it is an unwarranted assumption to think of a rhythmical or frequently interrupted nutrition. To which objection the answer may be, that whether we regard a rhythmic nutrition as the cause of rhythmic motion or not, we are obliged to hold such a method of nutrition as a fact. For we can be nearly certain that in the heart, as in other muscular, or any other parts, the successive impairments and renovations of composition, which constitute the process of nutritive maintenance, are severally accomplished during the successive periods of action and of repose, all exercise being attended with impairment of composition, such as can be repaired only during repose. Now the only repose of the heart's muscles, and I suppose of its nervous system also, is in the brief intervals between their successive actions; and in these intervals, and, therefore, with a rhythmic nutrition coordinate with its rhythmical action, the heart-structures must recover from the changes suffered

in their actions. Whether, then, as a cause, or as a consequence, where there is rhythmical action there must be corresponding rhythmical waste and repair; for we cannot reasonably suppose that the heart, or any other similarly acting organ, has, as a special prerogative, an exemption from the law of impairment in or by exercise: such an exemption is, indeed, inconceivable.

Now if rhythmic nutrition be thus proved as a necessary attendant of rhythmic action, it must be regarded as the cause, not the consequence, of the action; for in all cases nutrition has precedence of other actions in organized bodies; and the time-regulation of nutrition is a general and principal fact, and is a cause, not a consequence, of many phenomena which we trace in other organs than the heart, and many of which are attended with time-ordered movements.

I suspect that, to many, that which will seem most difficult of acceptance, is the belief that in so quick rhythmic actions as that of the mammalian heart (for example), or that of cilia, there can be a corresponding quickness of alternation of the progressive and retrogressive changes which essentially constitute nutrition. It must be admitted that, when we watch these movements, they appear, at first sight, very unlike anything that can result from nutritive changes, in which we are apt to think of a certain deliberation and quietness. But all rhythmic movements are not thus rapid; and when we watch the actions of a heart reduced to move only once in two or three minutes (as a frog's may be by ligature around the venous sinus), the appearance is like nothing more than it is like that of a process of nutritive changes, in which the structures gradually reach a climax of instability, and then quickly change. Whatever value then there may be in the appearance of a rhythmic action as an indication of its cause, it might be adduced on either side of the inquiry.

But let me add, that the nutritive changes to which I here refer, do not involve the supposition of any rapidly successive making and unmaking of the structures of the rhythmic organ, whether the heart or any other. We have probably held too much of the making and unmaking of elemental parts as essential to their maintenance by nutrition. In the modelling of parts during development and growth, such complete changes probably occur; but in mere maintenance of parts there is no evidence of their frequent or ordinary

occurrence, and to assume it is contrary to the fact, that we rarely find any rudimental structures among the perfect ones. In the most active muscles of the adult, for example, I doubt whether a rudimental or developing fibre could be found; we have sufficient chemical evidence of a constant change of material in them, but no evidence of an equal or parallel change of structure. And so in the blood: the change of material is very rapid, but the change of structures, which we may in some measure estimate by the proportion of white or rudimental blood-cells, is probably slow*. And again, in the secreting glands, excepting those of the skin and the breasts, we have no evidence, and, I think, no sufficient reason to believe, that in all cases the gland-cell-walls dissolve or burst in the act of secretion, so as to need the entire new formation of fresh cells. For we find in most of the active glands no considerable number of either rudimental or degenerate cells; and the observations of Ludwig and Rahn on the secretion of saliva indicate, as many other facts do, that in ordinary secretion (which is the ordinary nutrition of glands) the cell-contents, gradually transformed, flow out through the persistent cell-walls.

Nutritive maintenance, then, probably requires nothing more than molecular substitution. Atoms even of the refuse substance may be passing out, and atoms of the renewing substance passing into places among the structures of a comparatively persistent framework. Cell-walls or their analogues may be long-lived, while their contents are undergoing continual mutation. Such a process of molecular interchange and passage is, indeed, visible in the absorption of oil through the epithelial cells and villi of the intestines; and this is probably only a coarse example of the ordinary manner in which cells change their contents in the nutritive processes. Changes like these may well consist with the quickest rhythmic action.

I would thus, then, conclude as to the most probable explanation of the rhythmic action of the heart:—

1. In the Vertebrata it is due to the time-regulated discharges of

* The very small quantity of iron, in proportion to the quantities of the other constituents of the blood-cells, found in the excretions, is another indication of the comparatively slow waste of the red blood-cells, and may suggest, besides, that in nutritive maintenance there is not an equal mutation of all the component substances of a structure.

nerve-force in certain of the ganglia in and near the substance of the heart, by which discharges the muscular walls are excited to contraction.

2. In Invertebrata, the corresponding pulsatile movements of hearts or vessels are probably independent of nerve-force.

3. The time-regulated rhythmic action, whether of the nervous centres or of the independent contractile walls, is due to their nutrition being rhythmic, *i. e.* to their being, in certain periods, by nutritive changes of composition, raised, with regulated progress, to a state of instability of composition, in their decline from which they discharge nerve-force, or change their shape, contracting.

4. The muscular substance of the heart in the Vertebrata, governed in its rhythmic action by appropriate nervous centres, has a rhythmic nutrition of its own, corresponding and coordinate with theirs; the impairments of its structure during action being repaired in repose.

5. Rhythmic nutrition is a process in accordance with the general laws of organic life, very many organic processes being composed of timely-regulated alternate action and inaction, or alternate opposite actions, *i. e.* being rhythmical, with larger or shorter units of time; and all organic processes being chronometric, *i. e.* ordered according to laws of time as exact, and only as much influenced by external conditions, as are those relating to weight, size, shape, and composition.

June 15, 1857.

The LORD WROTTESLEY, President, in the Chair.

The following gentlemen were admitted into the Society:—

The Rev. T. Romney Robinson, D.D.
Lionel Smith Beale, Esq.
George Grote, Esq.
Rowland Hill, Esq.
The Rev. Thomas Kirkman.
William Marcet, M.D.
John Marshall, M.D.
Andrew Smith, M.D.
John Welsh, Esq.